Universidade de Aveiro Departamento de Biologia
2015

Luís Pedro Pratas Branco Santiago

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Dissertação apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Mestre em Ecologia Aplicada, realizada sob a orientação científica do Professor Doutor António José Arsénia Nogueira, Professor Associado com Agregação do Departamento de Biologia da Universidade de Aveiro e do Professor Doutor Wilson Roberto Spironello, Professor e Investigador do Instituto Nacional de Pesquisas da Amazónia.

Este estudo foi desenvolvido com o apoio logístico e institucional do Instituto Nacional de Pesquisas da Amazónia e pela Universidade de Aveiro financiado pela parceria entre a Conservation International, The Missouri Botanical Garden, The Smithsonian Institution and The Wildlife Conservation Society e The Gordon and Betty Moore Foundation.

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Agradecimentos

Ao Grupo de Pesquisas de Mamíferos da Amazónia do INPA, pelo ambiente que proporcionavam dentro da sala e pela alegria que era ir trabalhar e discutir os mais diversos assuntos com vocês, e pela ajuda fundamental que deram na montagem e desmontagem de câmeras. Em especial, ao Professor Wilson Spironello (Rei-Imperador) e ao meu eterno companheiro de selva André Gonçalves pela amizade e por terem sido incansáveis para que os levantamentos se realizassem e tudo o que me ensinaram nos últimos três anos. Obrigado por terem sido os meus mentores!

Ao Ronis Da Silveira pelos ensinamentos que me transmitiu também este ano, apesar de desta vez não termos tido oportunidade de ter tanto contacto.

Ao Professor Doutor António José Arsénia Nogueira por me ajudar a voltar à selva e por todo o apoio e preocupação demonstrados por mim desde o início do processo.

Ao INPA, à Universidade de Aveiro, Conservation International, The Missouri Botanical Garden, The Smithsonian Institution, The Wildlife Conservation Society e Gordon and Betty Moore Foundation por todo apoio logístico, institucional e financeiro que providenciaram.

Ao Kei Matsushima e ao Raimundo, por me terem acompanhado pelo meio do mato, em especial ao Raimundo por me ter alertado para a surucucu (*Lachesis muta*) que se cruzou no meu caminho.

À minha família pelo apoio a todos os níveis que me deram, em especial à minha mãe Margarida Maria Miranda Pratas pelo incentivo constante nos últimos 7 anos que passei fora de casa, que culminaram nesta dissertação.

A todos os meus amigos de Aveiro por todas as loucuras e momentos bonitos que me proporcionaram ao longo dos meus tempos de estudante. Obrigado à minha família académica, a Família do Absinto, em especial à minha patroa Filipa Domingues, ao meu irmão de praxe Miguel “Naruto” Monteiro e aos meus pedaços (e ao Manteigas), à malta da PILA, do Sarcófago e da Paródia. Agradeço especialmente também a Jotó Barão da Nóbrega, Filipa Domingues e à Inês Poca por se terem disponibilizado para me ajudar, lendo a minha dissertação.

A todos os meus amigos de Lisboa, especialmente à Pimpas, aos Jamantas e Paparoukos, por andarem sempre por perto, apesar de estarem a um oceano de distância.

Ao pessoal da minha casa Rodolfo, Diego e Molly (e frequentadores assíduos – Régis, Fábio Mattos, Carlos Demeterco e Danilo), por terem sido a minha família este ano e pela união, que me fez sentir em casa. Em especial à Molly-ann Louise Barnett por ter estado sempre ao meu lado e por me ter ajudado com o inglês.

Ao Careta e a todas as pessoas do Lago Amanã, que me proporcionaram um Natal extremamente aconchegante e uma fantástica aventura nesse lugar mágico no coração da Amazónia.

E por fim aos bichos e à selva!

Todos vocês fizeram de mim melhor biólogo e pessoa.

Palavras-chave

Amazónia, horários, lua, mamíferos, ocelotes, padrões de actividade, predador-presa, pumas, risco de predação, sobreposição temporal.

Resumo

Na relação predador-presa as adaptações no nicho temporal desempenham um papel de relevo na estruturação das comunidades. Nesta dissertação, foram investigados, através de armadilhagem fotográfica, os efeitos do ciclo lunar nos horários de actividade de ocelotes (*Leopardus pardalis*), pumas (*Puma concolor*) e das suas potenciais presas, na Amazónia Central. Neste trabalho testámos a sincronização dos padrões de actividade dos ocelotes com os das suas potenciais presas diurnas e nocturnas e os efeitos do ciclo lunar nesta relação predador-presa. Descrevemos também os padrões de actividade de pumas e avaliámos a influência do luar nos horários de actividade das presas destes felinos, em diferentes fases da lua.

Os ocelotes mostraram um padrão de actividade nocturno e o número de registos fotográficos manteve-se constante ao longo do ciclo lunar. Além disso, estes felinos revelaram ter um valor de sobreposição temporal de actividade significativamente maior com as suas presas nocturnas do que com as diurnas, durante a lua cheia.

Também os pumas mostraram ser maioritariamente nocturnos e a sua distribuição de registos fotográficos foi constante ao longo do ciclo lunar. Esta distribuição também foi observada para o veado-mateiro (*Mazama americana*). Por outro lado, os registos fotográficos das outras duas potenciais presas (pacas [*Cuniculus paca*] e armadilhos [*Dasypus* spp.]) estiveram concentrados em noites mais escuras. De qualquer forma, apesar destas diferenças, todas as presas parecem evitar as horas mais iluminadas da noite, independentemente da fase da lua.

Resumo (cont.)

Os nossos resultados sugerem que, em noites iluminadas, as presas podem suprimir ou alterar a distribuição temporal das suas actividades, deslocando-as para horas mais escuras da noite em resposta a um aumento do risco de predação. Por outro lado, é possível que pumas e ocelotes tirem proveito das presas que permanecem activas nessas noites, pois estas ficarão mais vulneráveis, aumentando o sucesso de caça destes felinos.

Keywords Activity patterns, Amazon, mammals, moon, ocelots, predation risk, predator-prey, pumas, temporal overlap.

Abstract

Between the predator-prey relationships, adaptions in the temporal niche play a significant role in the community structure. In this dissertation we investigated the effects of the moon cycle on the activity time schedules of ocelots (*Leopardus pardalis*), pumas (*Puma concolor*) and their potential prey, in Central Amazon. In this work, we tested whether the activity patterns of ocelots are synchronised with those of their potential diurnal and nocturnal prey and the effects of the moon cycle on this predator-prey relationship. In addition we described pumas activity patterns and assessed the influence of moonlight on the time schedules of their prey, in different moon phases.

Ocelots have shown to be nocturnal and their photographic records were evenly distributed across the moon cycle. The activity of these cats overlapped significantly more that of their nocturnal prey than diurnal's, during full moon.

Pumas were shown to be mostly nocturnal and have an even record distribution over the moon cycle too. This record distribution was observed for red brocket deer (*Mazama americana*) as well. In contrast, photographic records of the other two potential prey (pacas [*Cuniculus paca*] and armadillos [*Dasypus* spp.]) were concentrated in the darker nights. Yet, every potential prey seemed to avoid the brighter times of the night regardless of the moon phase.

Abstract (cont.)

Our findings suggest that, in enlightened nights, prey can suppress their activity or shift its temporal distribution, through activity allocation to the darker periods of the night in response to increased predation risk. On the other hand, pumas and ocelots may take advantage of prey which remain active in those nights because they will be much more vulnerable and, thus, favour the hunting success of these cats.

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INTRODUCTION

Animals may adapt their activity patterns throughout the circadian cycle in order to increase their fitness and allow their mutual coexistence (Schoener, 1974). It is known that the temporal distribution of behaviour can also shift under different conditions (Daan, 1981). The nocturnal bottleneck hypothesis states that all mammals share a common nocturnal ancestor (Hut *et al*., 2012). Early mammals are thought to have developed endothermia in order to occupy the nocturnal temporal niche to avoid ectothermic predators and competitors, such as dinosaurs (Hut *et al*., 2012; Gerkema *et al*., 2013). Due to the extinction of these reptiles, mammal species were able to expand and diversify their temporal niches (Hut *et al*., 2012).

Cats are the major predators across the world. As predators they play a major role within the food chains regulating the numbers of prey and maintaining the ecosystems' diversity and balance (Treves & Karanth, 2003; Cheida *et al*.; Michalski *et al*., 2006). Between the predator-prey relationships, niche adaptions play a significant role in the coexistence of species and community structure, since predators modify their patterns to match their prey's (Harmsen *et al*., 2010). In turn, prey try to avoid the times when predators are more active (Lima & Bednekoff, 1999) or segregate in other niche dimensions (Lucherini *et al*., 2009).

Amongst abiotic factors, moon cycle is reported to play an important role in niche adaptions (e.g. Clarke, 1983; Lucherini *et al.*, 2009; Michalski & Norris, 2011). Several nocturnal animals change their activity patterns (Julien-Laferrière, 1997; Kotler *et al*., 2002; Mori *et al*., 2014) and habitat use (Emmons *et al*., 1989; Kotler, Brown & Hasson, 1991; Schwitzer *et al*., 2007; Penteriani *et al*., 2013) due to moon light and the level of that response classifies species as lunarphobic (Morrison, 1978) or lunarphilic (Gursky, 2003). For instance, rodents are known to reduce their activity in brighter nights (Clarke, 1983; Kotler *et al*., 1991), allocate it to darker periods of the night (Daly *et al*., 1992; Kotler *et al*., 2002, 2004) or seek for covered areas (Emmons *et al*., 1989; Kotler *et al*., 1991). This behaviour is thought to be due to an increment of predators hunting success during these nights (Morrison, 1978; Clarke, 1983; Kotler *et al.*, 1991; Mougeot & Betagnolle, 2000; Jetz, Steffen & Linsenmair, 2003). On the other hand, other species, such as primates, have

shown to be more active in the brighter times of the circadian and moon cycles and preferred more opened areas because they are highly-dependent on vision for predator detection, orientation and feeding (Nash, 1986; Fernández-Duque; Gursky, 2003; Schwitzer *et al*., 2007). Many remains still unknown, however, and a better perception of the responses of several taxa to moonlight is therefore required for a full understanding of its effects.

In this Master's dissertation we evaluated the effects of the moon cycle on the time schedules of ocelots (*Leopardus pardalis*), pumas (*Puma concolor*) and prey of these cats, in Central Amazon. The first chapter describes the daily activity patterns of ocelots and their prey. In addition, the amount of records of each nocturnal species and the temporal activity overlap between ocelots and different types of prey (diurnal and nocturnal) were also assessed in each moon phase. In the second chapter the allocation of daily activity of puma prey species was analysed in different moon phases. Besides, we tested whether pumas and prey prefer particular nights within the moon cycle. Both of these chapters comprise under revision manuscripts in the *Journal of Zoology*.

STUDY AREA

The present study was conducted in three primary *terra-firme* forest sites in Central Amazonia, considered protected areas and under the management of National Institute for Amazonian Research (INPA) located respectively at 26km (Adolpho Ducke Forest Reserve - ADFR; 02º 08'S, 60º02'W), 60km (Cuieiras Biological Reserve - CBR; 02º 37'S, 60º 09'W) and 80km (Biological Dinamics of Forest Fragments Project Reserve - BDFFP; 2º 30'S, 60º W) north from the city of Manaus, Amazonas State, Brazil (PELD, 2012; Fig. 1). The natural habitat in this region is composed by primary lowland Amazonian forest, whose canopy is 30-39 m height (Castilho *et al*., 2006; Oliveira *et al*., 2008) and the topography is marked by plateaus, several water streams, and average elevation of 40-160 m above sea level (Prance, 1990; PELD, 2012).

The region has a tropical wet climate, with average temperature of 26ºC and well-defined seasons, with most of the rain falling from December to May (211-300 mm monthly average), and a dry season occurring from June to November (42-162 mm monthly average) (Ribeiro & Adis, 1984).

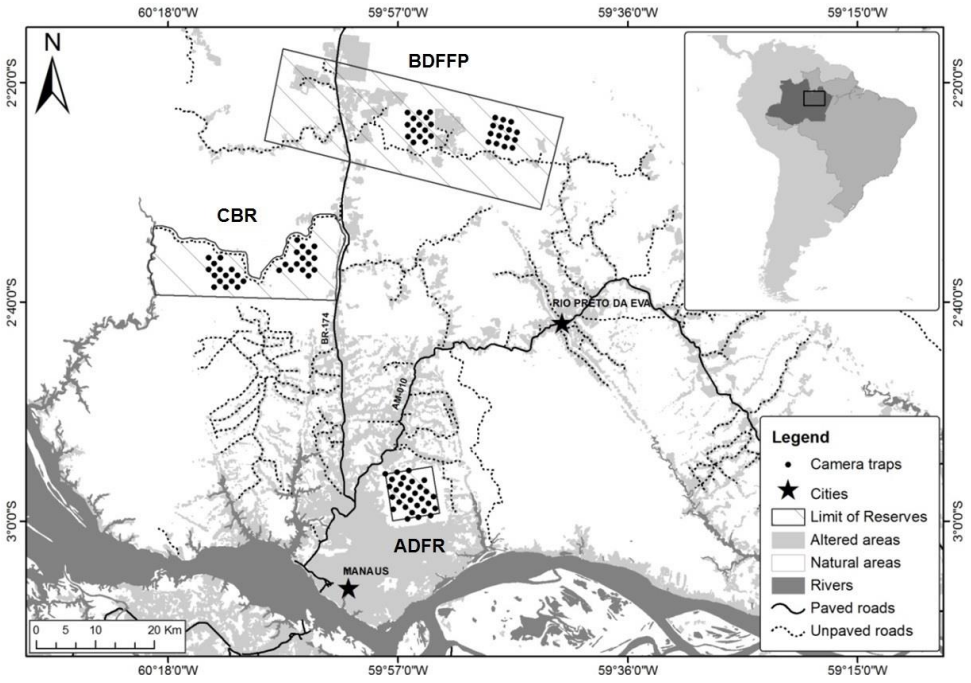

Figure 1. The trap station locations (black spots) in study sites located in Central Amazon, Amazonas State, Brazil.

CHAPTER 1 –The Moon Cycle Effect on the Activity Patterns of Ocelots and their Prey.

Abstract

The time of the activity may be changed throughout the circadian cycle in order to increase the fitness of species and allow their co-existence. The goal of this paper is to test whether the activity patterns of ocelots (*Leopardus pardalis*) are synchronized with those of their potential prey, and assess the effect of the moon cycle on this predator-prey relationship, through camera-trapping. Activity levels of ocelots and potential prey have been assessed across circadian and moon cycles and the temporal overlap between them was calculated for each moon phase. Ocelots have shown to be nocturnal and the number of their records has been constant across the moon cycle, and their activity patterns overlapped those of their nocturnal prey significantly more than remaining species', during full moon. These findings suggest that ocelots switch the type of prey (diurnal or nocturnal) they hunt in different moon phases and display higher hunting success in full moon nights.

KEY WORDS: Activity overlap, activity patterns, moon phases, predator-prey.

Introduction

Animals may adapt their schedules throughout the circadian cycle in order to increase their fitness and allow their mutual co-existence (Schoener, 1974). It is known that the activity patterns can be modified in response to several endogenous and/or exogenous factors (Daan, 1981). Species can show great temporal overlap if they segregate in other dimensions of the same niche (Lucherini *et al*., 2009). Between the predator-prey relationships, temporal adaptions play an important role in the community structure, since predators adjust their activity patterns to overlap those of their prey (Harmsen *et al*., 2010).

Moon cycle is reported to play a major role in activity changes and several nocturnal animals are able to alter their activity in response to moon light variation (e.g. Clarke, 1983; Penteriani *et al*., 2013). For instance, some mammals, such as small rodents (Clarke, 1983; Kotler *et al*., 1991) and bats (Morrison, 1978; Usman *et al*., 1980) are known to reduce their activity in brighter nights. This behavior is thought to decrease vulnerability, because predators are more effective in bright nights (Morrison, 1978; Clarke, 1983; Kotler *et al*., 1991; Mougeot & Betagnolle, 2000; Jetz, Steffen & Linsenmair, 2003). On the other hand, other species, such as some primates (Nash, 1986; Fernández-Duque; Gursky, 2003; Fernández-Duque, de la Iglesia & Erkert, 2010) and some nocturnal birds (Mills, 1985; Jetz *et al*., 2003; Wilson & Watts, 2006) are also known to be more active in brighter nights. This increment of activity may be related to both higher predator awareness and increased food uptake success (Mills, 1985; Nash, 1986; Gursky; Jetz *et al*., 2003; Wilson & Watts, 2006; Fernández-Duque *et al*., 2010). Therefore light is an important determinant of the activity of species.

Concerning Neotropical cats, studies regarding the effects of the moonlight on their activity patterns and their prey's usually target larger species (*Panthera onca* and *Puma concolor*; Harmsen *et al*., 2010). As for smaller species, ocelots (*Leopardus pardalis*) are reported as nocturnal (Caso *et al*., 2008), but at smaller scales they also have shown considerable temporal plasticity (Emmons, 1988; Crawshaw & Quigley; Konecny, 1989; Maffei *et al*., 2005; Di Bitetti, Paviolo & De Angelo, 2006). In the Peruvian Amazon, Emmons *et al*. (1989) found that during nights with contrasting moonlight levels, ocelots consistently overlapped the temporal activity of their main prey in the region (spiny rats *Proechimys* spp.), though they altered their habitat use. Little is known, however, about the effect of the entire moon cycle on the relationship between the activity patterns of ocelots and their prey. For these reasons, our goals were to test whether the activity patterns of ocelots are synchronized with those of their potential prey and if there is a moon cycle effect on those patterns.

Material and Methods

Sampling design

The trap stations were installed 2km apart from each other, arranged in a regular grid and following a well-established protocol for mammal monitoring from Tropical Ecology Assessment and Monitoring Network (TEAM) (TEAM, 2012). Reconyx Inc. (RM45 Hyperfire model) cameras were used and programmed to run for 24 hours per day without delay between photos. Every trap station was set up roughly 30cm above the ground, in locations with animal tracks. Thirty trap stations (one camera each) were established within each site and the surveys were conducted during dry season, in years 2010, 2011 and 2012. During each survey, traps remained in position for about 30 consecutive days (apart from Ducke reserve, where they were for about 60 days, in 2012). Trap stations were always set in the same geographic coordinates. No bait was used, to avoid disproportionate increases in the frequency of some species (O'Connell, Nichols & Karanth, 2011).

Prey species

It is known that ocelots prey mostly on small-sized prey (Emmons & Feer, 1997) but no study concerning the feeding habits of these cats in Central Amazonia is available up to date. Thus, a literature review has been made in order to select the most likely prey already reported in other studies and that are present in our sampling areas (Emmons, 1987, 1988; Tewes & Schmidly, 1987; Konecny, 1989; de Villa Mezza, Meyer & González, 2002; Tirelli, 2010). Selected species were mammals: the nine-banded and greater long-nosed armadillos *Dasypus novemcinctus* and *D. kappleri* (2.7 – 11.8kg; Emmons & Feer, 1997; due to the difficulty to differentiate these two species in the photos, they have been pooled together), common opossum *Didelphis marsupialis* (0.57 – 1.61kg; Emmons & Feer, 1997), brown four-eyed opossum *Metachirus nudicaudatus* (0.30 – 0.48kg; Emmons & Feer, 1997), gray four-eyed opossum *Philander opossum* (0.20 – 0.66kg; Emmons & Feer, 1997), spiny rat *Proechimys* spp. (0.15 – 0.55kg; Emmons & Feer, 1997); and ground-foraging birds: gray-winged trumpeter *Psophia crepitans* (1 - 1.50kg; Sherman, Kirwan & Sharpe, 2014), great tinamou *Tinamus major* (0.70 - 1.24kg; Cabot *et al*., 2014a), variegated tinamou *Crypturellus variegatus* (0.35 - 0.42kg; Cabot,

Jutglar & Sharpe; 2014b) and Ruddy quail-dove *Geotrygon montana* (0.09 - 0.15kg; Baptista *et al*., 2014).

Data analysis

At the end of the sampling periods, the memory cards were recovered and data from images were extracted using the specialized DeskTEAM software (http://www.teamnetwork.org/help-deskteam). In order to avoid pseudoreplication, an independent record of prey was defined as the one occurring 1h apart from any other and ocelots were individually identified by the spots pattern (Trolle & Kéry, 2003).

Statistics analyses were conducted on R-software version 3.1.2 (R Development Core Team 2011). Using the *Circular* package for R-software (Agostinelli & Lund, 2013), a Rayleigh test was conducted to test the distribution uniformity on the daily activity data to assess whether or not species exhibited a random activity pattern over the circadian cycle. Through *Overlap* package for R-software (Meredith & Ridout, 2014), kernel density estimation curves were used to describe the activity patterns of each species. Kernel density estimations are a non-parametric way to estimate the probability density function of a distribution of records (Linkie & Ridout, 2011). This function assumes that an animal is equally likely to be captured at any time as long as it is active (Linkie & Ridout, 2011). Sunrise and sunset times of each record date were acquired by Moonphase SH software (version 3) and an estimate of these times was calculated. The crepuscular hours were defined as ± 1h from sunrise and sunset.

Overlap coefficients between the daily activity patterns of both predator and potential prey were also estimated using *Overlap* package for R-software (Meredith & Ridout, 2014). The chosen estimator for overlapping was Δ_1, recommended for samples < 50 records and data were bootstrapped (10,000 samples) to extract 95% confidence intervals (CI) from the overlap coefficients (Ridout & Linkie, 2009; Meredith & Ridout, 2014). Overlap coefficients range from 0 (no overlap), if species have no common active period, to 1 (complete overlap), if the activity densities of two species are identical (Schmid & Schmidt, 2006). To complement the overlap coefficient informations concerning predator-prey daily activity a Mardia-Watson-Wheeler (MWW) test (Batschelet, 1981) was conducted to compare the 24h-distribution of records of ocelot and each prey species (Monterroso, Alves & Ferreras, 2014).

To assess the effect of the moon phase in the activity of mammals, Moonphase SH software, version 3.3 was used to classify moon phase of records, according to the percentage of visible moon surface, as follows: 0-25% (New Moon [New]), 25-75% (Waxing and Waning Moons [Wx and Wn]) and 75-100% (Full Moon [Full]). Then, Fisher Exact tests (two-tailed) were conducted in order to perform pairwise comparisons among record proportions of each moon phase, for nocturnal species.

Temporal overlap coefficients between ocelots and the type (diurnal or nocturnal) of potential prey in each moon phase were also estimated through *Overlap* package for R-software (Meredith & Ridout, 2014), using the same methodology mentioned above. Confidence intervals were extracted from these estimates and pairwise comparisons of the temporal overlaps were performed between ocelots and diurnal prey, and ocelots and nocturnal prey, in each moon phase. All the statistics analyses were conducted with a 95% confidence level.

Results

The total sampling effort obtained was 6,300 trap-nights. There were 1,504 independent records of ocelots (N = 33), armadillos (N = 162), common opossums (N = 279), brown four-eyed opossums (N = 284), gray four-eyed opossums (N = 36), spiny rats (N = 167), gray-winged trumpeters (N = 274), great tinamous (N = 125), variegated tinamous (N = 64) and Ruddy quail-doves (N = 80).

Daily activity patterns

The Rayleigh test for data uniformity revealed that ocelots followed a nocturnal pattern, showing peaks of activity at the first half of the night and at the dawn (Fig. 2; Tab. 1). Mammal prey were also shown to be nocturnal with several different peaks during the night (Fig. 2; Tab. 1). Conversely, the records of ground-foraging bird species have shown that most of the activity was concentrated during the day and crepuscular periods (Fig. 2; Tab. 1).

Table 1. Rayleigh uniformity test (Z) for the temporal activity of ocelots and their potential prey species. N is the number of records. (*) for a non-random distribution ($P < 0.05$).

Species	**N**	**Rayleigh test**	
		Z	P
Mammals			
Ocelots	33	4.33	0.01*
Armadillos	162	76.40	$< 1.00 \times 10^{-12}$ *
Common opossum	279	123.49	$< 1.00 \times 10^{-12}$ *
Brown four-eyed opossums	284	130.88	$< 1.00 \times 10^{-12}$ *
Gray four-eyed opossums	36	18.41	4.70×10^{-9} *
Spiny rats	167	47.73	$< 1.00 \times 10^{-12}$ *
Birds			
Gray-winged trumpeters	274	92.42	$< 1.00 \times 10^{-12}$ *
Great tinamous	125	15.41	2.00×10^{-7} *
Variegated tinamous	64	15.44	1.90×10^{-7} *
Ruddy quail-doves	80	23.27	7.80×10^{-11} *

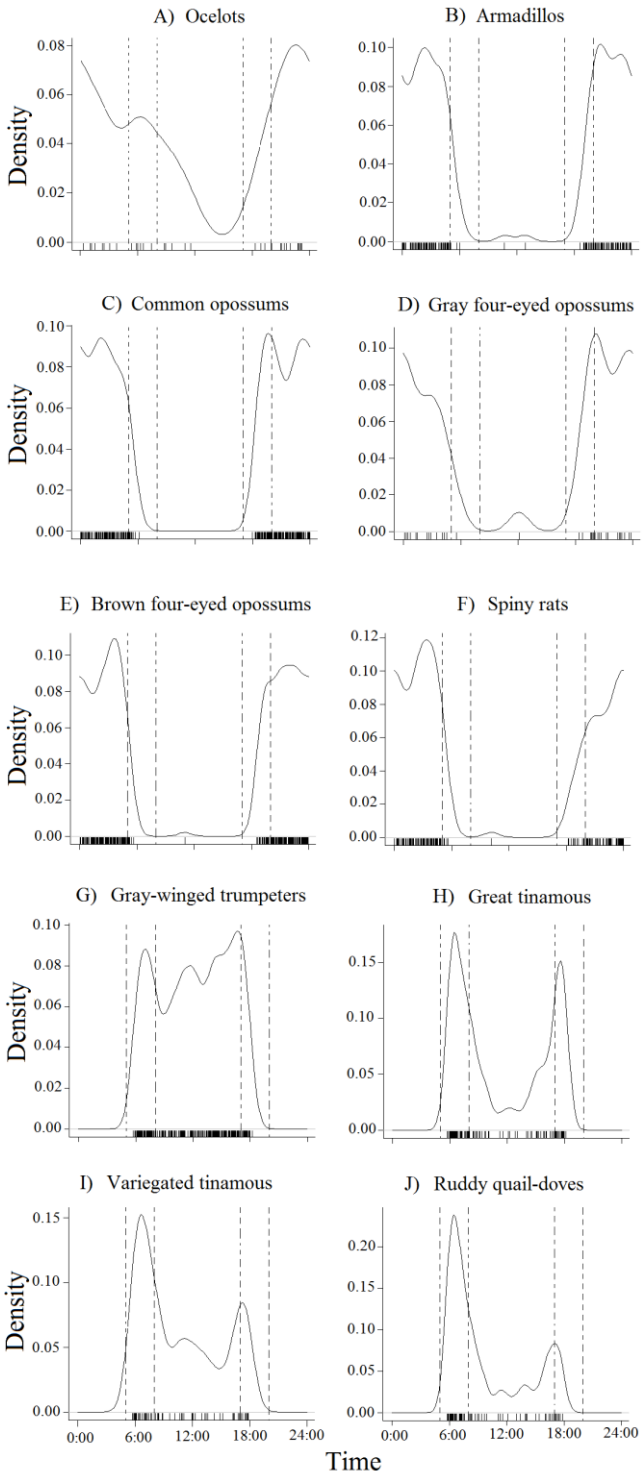

Figure 2. Daily activity patterns of A) ocelots, B) armadillos, C) common opossums, D) brown four-eyed opossums, E) gray four-eyed opossums, F) spiny rats, G) gray-winged trumpeters, H) great tinamous, I) variegated tinamous and J) Ruddy quail-doves. Time intervals between dashed lines for crepuscular periods of the day: 5:00 to 7:00 and 17:00 to 19:00 are Dawn and Dusk, respectively.

The overlap coefficients between the activity of ocelots and mammal prey were high and the MWW tests showed no differences between their daily distributions of records (Tab. 2). In contrast, bird prey were found to have intermediate overlap values (Tab. 2) with the activity of ocelots, with different record distributions (Tab. 2).

Table 2. Overlap coefficient (Δ_1) between ocelots and their potential prey, 95% confidence intervals (95% CI) and Mardia-Watson-Wheeler test (W). (*) when distribution of records is significantly different from that of the ocelots ($P < 0.05$).

Mammals	**Δ_1 (95% CI)**	**W**	**P**
Armadillos	0.70 (0.56-0.82)	4.30	> 0.05
Common opossums	0.71 (0.55-0.82)	3.39	> 0.05
Brown four-eyed opossums	0.70 (0.55-0.81)	4.17	> 0.05
Gray four-eyed opossums	0.72 (0.55-0.85)	2.07	> 0.05
Spiny rats	0.70 (0.54-0.82)	5.85	> 0.05
Birds			
Gray-winged trumpeters	0.40 (0.25-0.52)	37.39	7.60×10^{-09} *
Great tinamous	0.42 (0.26-0.51)	23.92	6.40×10^{-06} *
Variegated tinamous	0.46 (0.27-0.58)	22.34	1.40×10^{-05} *
Ruddy quail-doves	0.40 (0.24-0.51)	23.48	7.90×10^{-05} *

Moon phase

Ocelots and gray four-eyed opossums were the only nocturnal species with a uniform distribution across moon cycle (Fig. 3). The number of records of armadillos increased during the new moon (Fig. 3), contrasting with a decreasing at waxing phase of common opossum records (Fig. 3). Differences were also observed for brown four-eyed opossums, whose records were higher in new and full moons, and spiny rats, which had more records at new moon (Fig. 3).

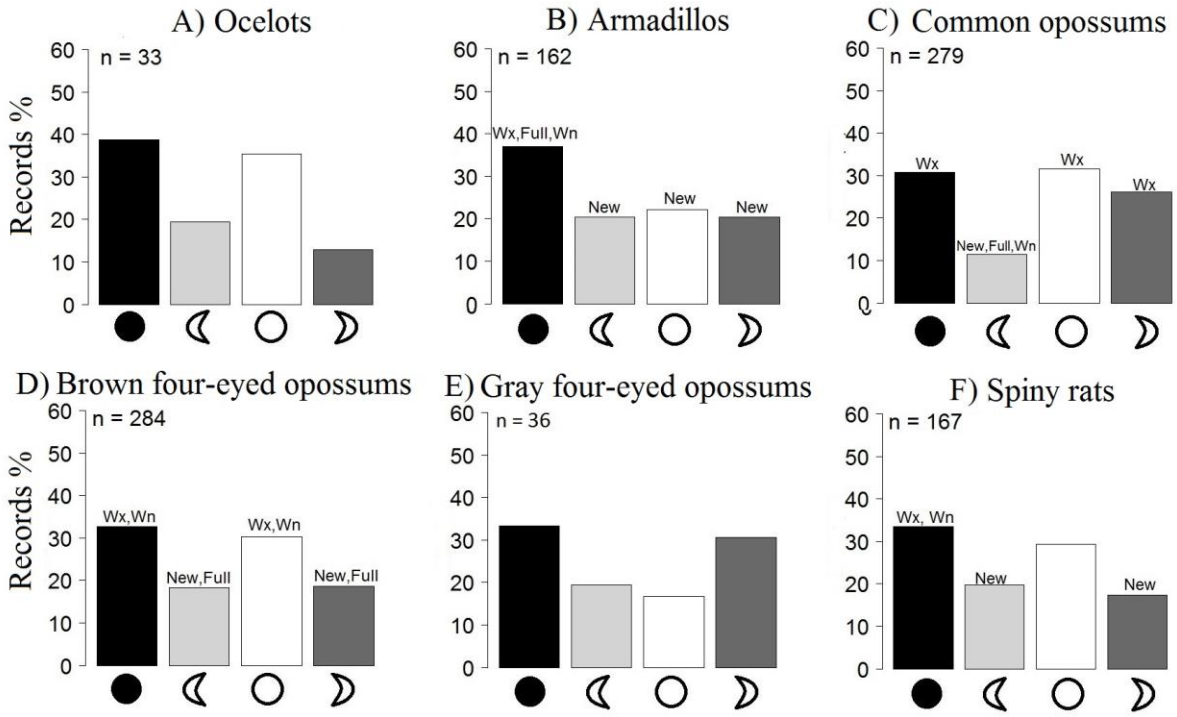

Figure 3. Proportion of records of A) ocelots and their nocturnal prey: B) armadillos, C) common opossums, D) brown four-eyed opossums, E) gray four-eyed opossums, F) spiny rats, in different moon phases: New Moon (●); Waxing Moon (☾); Full Moon (○); Waning Moon (☽). Results of Fisher Exact test: New – significantly different from New Moon; Wx – significantly different from Waxing Moon; Full – significantly different from Full Moon; Wn – significantly different from Waning Moon.

The activity of the ocelots overlapped significantly more with the activity of nocturnal prey than with that of the diurnal ones, during the full moon (Tab. 3).

Table 3. 95% confidence intervals (95% CI) of overlap between ocelots and their diurnal and nocturnal prey species, in each moon phase. (*) for statistically significant differences between overlap values of the activity of ocelots with that of diurnal and nocturnal prey species.

		Diurnal prey	Nocturnal prey
Moon phase		**Δ_1 (95% CI)**	**Δ_1 (95% CI)**
New	●	0.34 (0.15 – 0.56)	0.72 (0.51 – 0.87)
Waxing	☾	0.41 (0.12 – 0.70)	0.57 (0.28 – 0.81)
Full	○	0.22 (0.07 – 0.42)*	0.80 (0.62 – 0.91) *
Waning	☽	0.59 (0.23 – 0.85)	0.37 (0.07 – 0.67)

Discussion

Daily activity patterns

Birds have shown expected diurnal and crepuscular patterns due to their dependence on vision (Daan, 1981) and the temporal distribution of their records followed the same pattern of previous studies on ground-dweller species (Skutch, 1963; Blake, 1992; Brooks *et al*., 2001; Nijman, 2007; Selvan *et al*., 2013). In contrast, mammal prey showed to be strongly nocturnal, which may be connected to predator and competition avoidance behaviours (e.g. Clarke, 1983; Cardoso & dos Santos, 2014) and higher temperatures during the daylight time (Marcomini & Oliveira, 2003).

The nocturnal activity pattern and temporal distribution of ocelots records we observed matched with nocturnal prey records and not with diurnal prey's, as was previously reported in the Peruvian Amazon (Emmons, 1987, 1988). Most of the predators activity patterns mostly coincide with prey's (Fedriani, Palomares & Delibes, 1999; Harmsen *et al*., 2010; Foster *et al*., 2013) and ocelots are known to prey chiefly on nocturnal mammals (Emmons, 1987). However, even though ocelots have a different distribution of records than birds', they also seem to have an important degree of diurnality, showing an intermediate overlapping with diurnal prey activity. In fact, ocelots are also known to prey on diurnal birds (Emmons, 1988) and vary their patterns

considerably across their range (Crawshaw & Quigley; Konecny, 1989; Maffei *et al*., 2005; Di Bitetti *et al*., 2006). Thus our findings are likely to reflect the opportunistic feeding habits (Emmons, 1987; Aliaga-Rossel *et al*.; Moreno, Kays & Samudio, 2006; Bianchi & Mendes, 2007; Bianchi, Mendes & Júnior, 2010) and ecological plasticity of these cats (Caso *et al*., 2008).

Moon phase

Nocturnal animals responded differently to moon light. Armadillos and spiny rats were more active at new moon. Some authors suggest that greater activity on darker nights decreases mortality rates due to nocturnal predators which are at least partially orientated by vision, beyond hearing and olfaction (Clarke, 1983; Kotler *et al*., 1991; Harmsen *et al*., 2010). Moreover, armadillos are not so active in bright moon phases because they lack on *tapetum lucidum* (McDonough & Loughry, 2013), an intraocular structure that increases retinal sensitivity (Schwitzer *et al*., 2007), and, thus, they are not able to spot their predators. Opossums are likely to experience a decrease in the predation risk in new moon as well, but they have also shown to be equally active at full moon. We suggest that the presence of *tapetum lucidum* in the marsupial ocular structure (Johnson Jr., 1997; Carpi, 2008) combined with greater insect uptake in full moon (Gursky; Jetz *et al*., 2003; Lessa & Geise, 2014) overwhelms the predation risk and provides conditions for opossums to be active in this moon phase too. This may not be the case for brown four-eyed opossums during moon phases with intermediate light levels, which suggests that somehow they perceive a higher predation risk or are more exposed to predation in these times of the moon cycle than the other opossum species.

Ocelots seemed to be little affected by moon cycle, following a similar pattern to other studies in rainforest (Emmons *et al*., 1989; Di Bitetti *et al*., 2006; Harmsen *et al*., 2010). On the one hand this may be due to a low number of ocelot records. On the other hand, this may also reflect a modification on their habitat use. In Peruvian Amazon ocelots did not alter their temporal activity during full moon but sought for vegetation cover to remain unseen, since they are ambush predators (Emmons *et al*., 1989). In order to find enough prey, ocelots spend most of their time hunting (Emmons, 1987). The uniform amount of records across the moon cycle therefore suggests that in different moon phases

they adapt their hunting tactics, although the number of ocelot records may also explain these results.

The daily activity of predators mostly coincides with that of their prey (e. g. Fedriani *et al*., 1999; Foster *et al*., 2013). Since ocelots prey mostly on small mammals, and most of those are nocturnal (Emmons & Feer, 1997), a strong overlap between predator and nocturnal prey would be expectable during all moon cycle. However, only during the full moon the temporal overlap with their prey was higher between nocturnal than diurnal species. Prey are not easily spotted and are highly disperse in dense forest leading to long time periods spent searching for prey due to the unpredictability of encounters (Emmons, 1987). Consequently we suggest that, aside from the full moon, diurnal activity is meant to compensate the lack on hunting success overnight in the remaining moon phases (Cozzi *et al*., 2012). As for full moon Emmons *et al*. (1989) suggested that ocelots' hunting success did not increase in moonlit nights because their main prey in their study area, the spiny rats, were hidden under cover. On the other hand, alternative nocturnal prey, such as opossums, have shown to remain on trails during brighter nights (Di Bitetti *et al*., 2006). Greater availability of arthropods during moonlit nights (Gursky; Jetz *et al*., 2003) is likely to make these insectivorous prey (Emmons & Feer, 1997) to be more exposed to attacks and therefore increase the hunting success of ocelots in these nights. Moreover, ocelots feed mostly on less than 1kg mammals, but such prey as common opossums may represent a great energetic uptake, releasing the cats from diurnal activity during full moon. Plus, ocelots are likely to get a positive trade-off between foraging benefits and being active on moonlit nights, when they can be seen by pumas more easily, because they are able to spot them as well (Emmons *et al*., 1989). We therefore suggest that ocelots switch their type of prey (diurnal or nocturnal) they hunt in different moon phases, their hunting efficiency increases in full moon and the greater foraging benefits they take in brighter nights outweigh the costs of being exposed to larger competitors.

The characteristics of ecological niche of ocelots are known to vary through their range (de Oliveira *et al*., 2010) and our study provides the first insights on the activity patterns of these cats and their potential prey in Central Amazon *terra-firme* forests. Still, one must be careful interpreting our results, since the number of ocelot (and gray four-eyed opossum) detections seems to be low against the number of trap-nights. In other rainforest

locations the number of records of this species is higher (e. g. Di Bitetti *et al*., 2006; Harmsen *et al*., 2010). This is likely to be, however, due to a natural feature in Central Amazon. Emmons (1984) suggested Central Amazon is a low productivity region and therefore it carries mammal populations at low densities. Carnivores are naturally sparse and along with Emmons (1984) hypothesis they probably occur at even lower abundance in this region. Moreover, carnivore detections are known to be lower in isolated areas with narrow and recently opened trails (Dillon & Kelly, 2007; Sollmann *et al*., 2012). Still, these areas are the locations where more studies are required because many of them are unexplored and many aspects concerning fauna remain unknown. Thus, further research on the adaptations of predators and prey for their coexistence is needed and will provide more knowledge regarding the ecology of these species and their relationship in this region.

Chapter 2 – Temporal dodging: How Does the Moon Phase Affect Activity Time Schedules of Puma Prey?

Abstract

Animals can adapt their activity patterns throughout the circadian cycle in order to increase the fitness of species and allow mutual coexistence. Prey may use moonlight as a surrogate of predation risk. Here we assessed moonlight influence on the activity time schedules of potential nocturnal prey of puma (*Puma concolor*), among different moon phases, through camera-trapping. Prey and pumas record distributions were assessed across the moon cycle and daily activity patterns of prey species were described in each moon phase. The record distribution of pacas (*Cuniculus paca*) and armadillos (*Dasypus* spp.) were concentrated in darker nights, contrasting with pumas and red brocket deer (*Mazama americana*), whose records were evenly distributed. Yet, every potential prey seemed to avoid the brighter times of the night regardless of the moon phase. These findings suggest prey can shift the temporal distribution of their activities under different moon phases, perhaps in response to predation risk variations.

KEY WORDS: Activity patterns, mammals, moon, predation risk.

Introduction

Species can alter their circadian activity patterns in response to several factors in order to increase their fitness (Daan, 1981). These modifications play a major role in the community structure because species can often coexist if their activity patterns are different (Schoener, 1974). Adaptions in the activity patterns are specially important if you consider competition, prey acquiring and predation risk (e.g. Colquhoun, 2006; Lucherini *et al*., 2009). Abiotic factors, such as weather, seasonality and light conditions may also

affect activity patterns (Crawshaw & Quigley, 1991; Daan, 1981; Maestri & Marinho, 2014).

Moonlight is an important abiotic determinant of the activity of nocturnal species (e. g. Kotler *et al*., 1991; Penteriani *et al*., 2013), because moon brightness changes between different phases and times of the night. Among nocturnal mammals, species are known to react differently to the moon light. In response to higher predation risk periods, many rodents allocate their activities to the darker times of the night (Daly *et al*., 1992; Kotler *et al*., 2004, 2002; Wolfe & Summerlin, 1989). In contrast, some primates allocate their activity to the brighter times of the night because they rely heavily on vision for predator detection, as well as feeding (Fernández-Duque; Gursky, 2003; Nash, 1986; Schwitzer *et al*., 2007).

Prey activity heavily relies on predation risk (Fernández-Duque, 2003; Oliveira-Santos, Tortato & Graipel, 2008). Predators try to synchronise their activity time schedules with those of their prey (Fedriani *et al*., 1999; Foster *et al*., 2013). To counter this temporal pursuit, prey develop anti-predatory strategies, such as increased vigilance at high predation risk periods and/or allocation of activity to low risk periods (Brown; Lima & Bednekoff, 1999). In southern Amazon Michalski & Norris (2011) suggested that pacas (*Cuniculus paca*) perceive moonlight as an increase in predation risk and allocate their activities to the darker hours of the night in more illuminated nights.. Little is known about the moon phase effect on the activity time schedules of other medium and large-sized mammals. A better perception of how moon cycle drives the activity time schedules of these animals is therefore important to understand their ecology and carry out conservation plans, if necessary. For these reasons, we assessed the moonlight influence on the daily activity patterns of several medium and large-sized mammals, which are known to be greatly nocturnal and potentially preyed upon by pumas (*Puma concolor*) and tested whether these cats and their potential prey display any preference for particular nights of the moon cycle. Additionally, we outlined the circadian activity patterns of pumas, which were still not described in this region.

Material and Methods

Sampling design

The trap stations were installed 2km apart from each other, arranged in a regular grid and following a well-established protocol for mammal monitoring from Tropical Ecology Assessment and Monitoring Network (TEAM) (TEAM, 2012). Reconyx Inc. (RM45 Hyperfire model) cameras were used and programmed to run for 24 hours per day without delay between photos. Every trap station was set up roughly 30cm above the ground in locations with animal tracks. Thirty trap stations (one camera each) were established within each study site and the surveys were conducted from July to October, in years 2010, 2011, 2012, and from October 2014 to April 2015. During each survey, traps remained in position for about 30 consecutive days (apart from Ducke, where they remained in position for about 60 days, in 2012). Trap stations were always set in the same geographic coordinates. No bait was used, to avoid disproportionate increases in the frequency of some species (O'Connell *et al*., 2011).

Prey species

Pumas are generalist predators and prey on medium and large-sized mammals (Emmons & Feer, 1997). Up to date, no study concerning the feeding habits of these cats is available in Central Amazon. Then, a literature review was made (Emmons, 1987; Foster *et al*., 2010; Iriarte *et al*., 1990; Novack *et al*., 2005; Tirelli, 2010) in order to select the species, which are known to have nocturnal activity in the Neotropics (Emmons & Feer, 1997), that are common prey of pumas and present on our sampling areas. Selected species were: the red brocket deer (*Mazama americana*), paca (*Cuniculus paca*) and nine-banded and greater long-nosed armadillos (*Dasypus novemcinctus* and *D. kappleri*). The last two species were pooled together, due to the difficulty to differentiate them in the photos. Common opossum (*Didelphis marsupialis*) was used as control species, since it is known that it is not a regular prey of pumas (Emmons, 1987; Tirelli, 2010).

Data analysis

At the end of the sampling periods, the memory cards were recovered and data from images were extracted using the specialised DeskTEAM software (see more at

http://www.teamnetwork.org/help-deskteam) and recorded species were identified by two independent researchers. In order to avoid pseudoreplication, an independent record of each species was defined as the one occurring one hour apart from any other at the same trap station.

All statistics analyses were conducted on R-software version 3.1.2 (R Development Core Team, 2011). Using *Circular* package for R-software (Agostinelli & Lund, 2013), a Rayleigh test was conducted to test the distribution uniformity of puma and prey records to assess whether or not these species exhibited a random record distribution over the moon cycle.

Through *Overlap* package for R-software (Meredith & Ridout, 2014) kernel density estimation curves were used to describe pumas circadian activity patterns. Kernel density estimations are a non-parametric way to estimate the probability density function of a distribution of records (Linkie & Ridout, 2011). This function assumes that an animal is equally likely to be captured at any time as long as it is active (Linkie & Ridout, 2011). Sunrise and sunset times of each record date were acquired by Moonphase SH software (version 3) and an estimate of these times was calculated. The crepuscular hours were defined as ± 1h from sunrise and sunset.

Using *Circular* package for R-software (Agostinelli & Lund, 2013) Mardia-Watson-Wheeler (MWW) tests (Batschelet, 1981) were conducted to compare the distribution of records between moon phases which occur in opposite dates of lunar calendar (new moon vs full moon; 1st quarter vs last quarter), for each prey species.

Kernel density curves were also used, through *Overlap* package for R-software (Meredith & Ridout, 2014), to describe the activity patterns of prey in each moon phase (Meredith & Ridout, 2014). To assess the effect of the moon phase on the activity of mammals, Moonphase SH software, version 3.3 was used to determine on the calendar the nights (± 1 night) of all four moon phases (new moon, 1st quarter, full moon and last quarter) and calculate an average time for moon transit (when the moon is on the zenith and thus, apart from new moon, when there is greater nocturnal illumination) on those nights. Then, we selected the records from those particular nights to assess the effect of the moon light and positioning on the time schedules of each potential prey and control species, during each moon phase. All the statistical analyses were performed with 95% confidence level.

Results

The total sampling effort was 14,728 trap-nights. We obtained a total of 1,031 independent records (pumas = 31; red brocket deer = 123; pacas = 262; armadillos = 244; common opossums = 371) across all the sampling time. From these records, 501 independent records of the prey species were extracted from the nights with particular moon phases: new moon (red brocket deer = 10; pacas = 45; armadillos = 44; common opossums = 49), 1st quarter (red brocket deer = 11; pacas = 22; armadillos = 34; common opossums = 30), full moon (red brocket deer = 17; pacas = 8; armadillos = 14; common opossums = 45) and last quarter (red brocket deer = 17; pacas = 52; armadillos = 37; common opossums = 52).

Pumas were mostly cathemeral (Fig. 4).

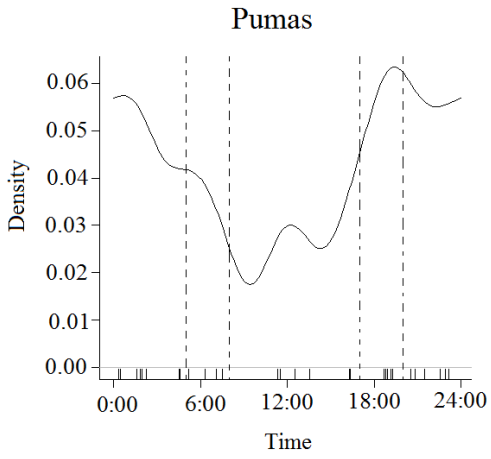

Figure 4. Daily activity patterns of pumas. Time intervals between dashed lines for crepuscular periods of the day: 5:00 to 7:00 and 17:00 to 19:00 are Dawn and Dusk, respectively.

The Rayleigh tests revealed that only pacas and armadillos have shown a non-random distribution of records through the moon cycle, giving preference to darker nights, contrasting with the remaining species, whose records were evenly distributed (Tab. 4).

Table 4. Rayleigh uniformity test (Z) for the records distribution throughout the moon cycle for pumas and their potential prey. (*) represents a non-random distribution ($p<0.05$). (Moon phase) for prey preferred phase when there is a non-random distribution across the moon cycle.

Species	**Moon cycle**		**Moon phase**
	Z	**P**	
Pumas	0.86	0.43	-
Red brocket deer	1.87	0.15	-
Pacas	21.01*	7.53×10^{-10}	Waning crescent
Armadillos	7.10*	8.29×10^{-4}	New moon
Common opossums	2.248	0.11	-

The distribution of records of every prey species was not significantly different between 1st and last quarters. However it differed between new moon and full moon for armadillos and showed a tendency for pacas (Tab. 5).

Table 5. MWW test (W) for record distribution of pumas' potential prey and control species between moon phases which occur in opposite dates of the lunar calendar (new moon vs full moon; first quarter vs last quarter). (*) represents significantly different distributions ($p<0.05$).

	New moon vs full moon		**1st quarter vs last quarter**	
Species	**W**	**P**	**W**	**P**
Red brocket deer	3.11	0.21	0.94	0.99
Pacas	5.78	0.06	0.01	0.99
Armadillos	15.92*	0.00	6×10^{-3}	1.00
Common opossums	0.4761	0.66	2.0×10^{-2}	1.00

In the new moon every species showed a uniform temporal distribution of records across daily cycle (Fig. 5). During the full moon deer had a major peak of records at dawn and the two remaining prey had their activity peaks at the first half of the night (Fig. 5). Additionally, armadillos had another peak at midnight on the most enlightened nights (Fig.

5). In contrast, common opossums showed a constant nocturnal activity in this moon phase (Fig. 5). Similarly, at the first quarter common opossums showed a constant activity through the night, contrasting with the remaining prey species (Fig. 5). Deer had a peak of activity on the middle of the night in this phase, differently from armadillos and pacas, which had more records in the second half of the night (Fig. 5). On the other hand, during the last quarter every prey was mostly active at the first half of the night, apart from deer whose records were more concentrated in the afternoon (Fig. 5).

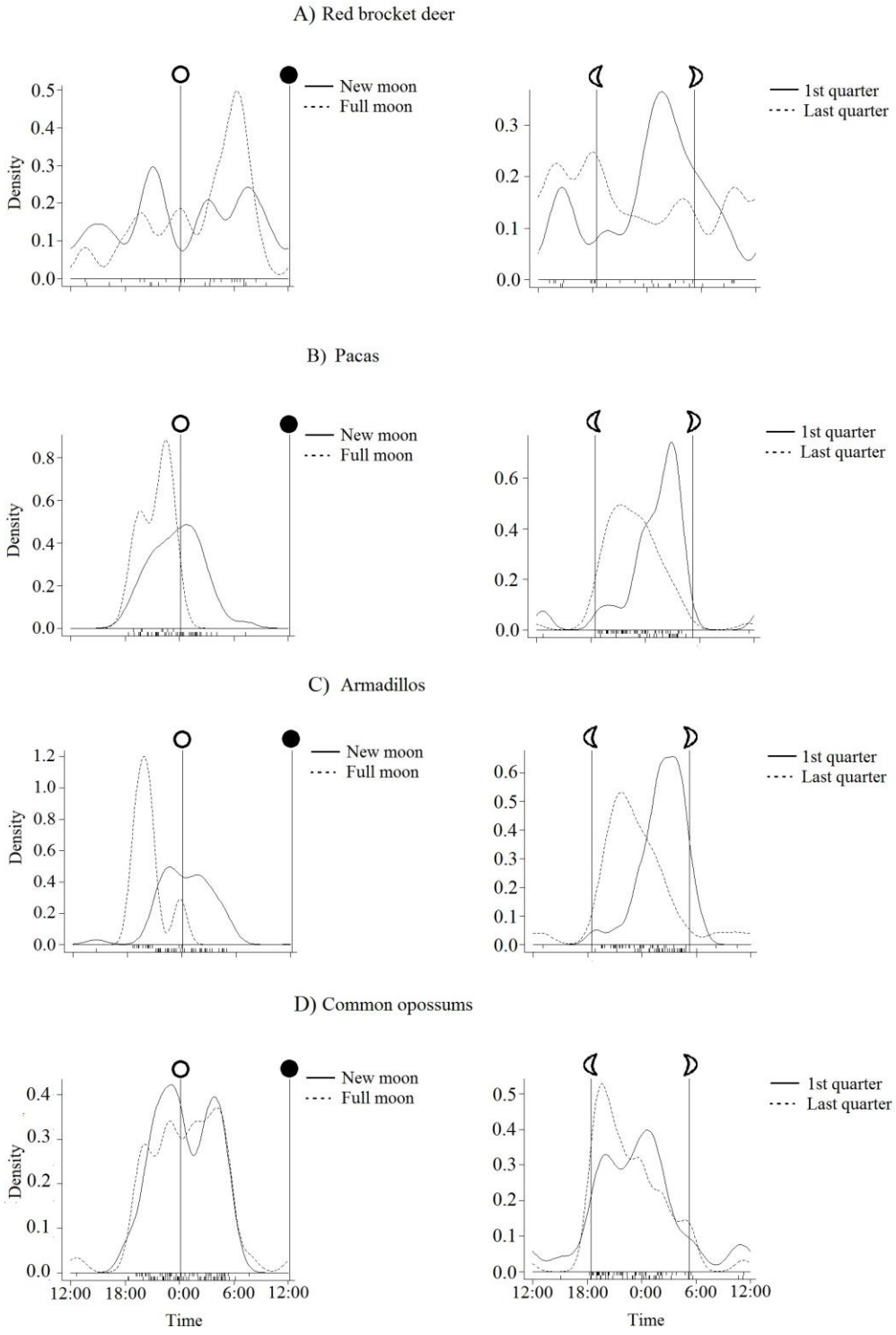

Figure 5. Daily activity patterns of potential nocturnal prey of pumas: A) red brocker deer, B) pacas, C) armadillos and the control species D) common opossums, during new moon, first quarter, full moon and last quarter. Vertical lines with ● , ☾ ,○ and ☽ on top represent the moon transit times at new moon, first quarter, full moon and last quarter, respectively.

Discussion

The response of nocturnal mammals to the moon light differs among taxa and may vary according to several determinants, such as phylogeny, trophic level, sensory systems and type of habitat (Prugh & Golden, 2014). Our study suggests that the moon phases are also likely to influence how prey distribute their activities through time in order to face different predation risk periods. Pacas and armadillos were already reported to show preference for darker nights due to lower predation risk (Harmsen *et al*., 2010). In contrast, red brocket deer showed no preference for any nights which may be due to activity allocation to diurnal periods in order to manage predation risk. The activity of pumas, which were found to be cathemeral in other Neotropical locations as well (Davis *et al*., 2010; Foster *et al*., 2013), was evenly distributed across the moon cycle too. It was expected that the activity distribution of these opportunistic cats through the moon cycle was unaffected (Harmsen *et al*., 2010). In the Belizean rainforest Harmsen *et al*. (2010) suggested that pumas do not alter their activity between different moon phases, but spend their time in different hunting areas to take any prey they can find. An alternative explanation may arise from the even activity distribution of pumas over the moon cycle. Even though pumas are opportunistic predators (Iriarte *et al*., 1990), in the rainforests they seem to have a certain degree of preference for deer (*Mazama* spp.: 9.0 – 14.10% occurrence in scats; Foster *et al*., 2010; Novack *et al*., 2005; and *Odocoileus* sp.: 10.90% occurrence in scats; Novack *et al*., 2005). It is known that the activity of specialised predators is associated with their prey's through the moon cycle (Penteriani *et al*., 2013). Therefore we cannot exclude that the even distribution of puma records through the moon cycle may be associated as well to the red brocket deer's, since this species was recorded evenly through the moon cycle too.

Lunarphobic prey perceive a higher predation risk with moonlight (Kotler *et al*., 1991). As nocturnal illumination levels differ between times of the night during different moon phases, variation on the predation risk through the night is expectable. Small mammals were reported to increase their activity in darker nights due to a decrease of predators' efficiency (Clarke, 1983; Kotler *et al*., 2010, 1991 Penteriani *et al*., 2013). Our findings suggest that in the new moon the predation risk is so low that it allows prey

species to be active uniformly during the whole night. On the other hand, in the other three moon phases, prey species may have to allocate their activity to times of the night when predation risk is lower (Michalski & Norris, 2011). Although armadillos were the only species whose record distribution was different between new and full moons, every other potential prey seems to avoid the brighter times of the night, regardless of the moon phase. During the full moon, we observed that every prey species tends to concentrate their activities in the first half and in the end of the night, when the moon is more distant from the zenith and thus the moonlight is less intense. In contrast, the record distribution of common opossums was similar in both new and full moon phases. These results were expected, since in the southern and western Amazon, common opossums are known to be rarely taken by cats (Emmons, 1987; Tirelli, 2010). Hence, the distinct record distribution of prey between the darker and brighter moon phases suggests a greater predation risk for these species at the middle of the full moon nights, when there is the greatest nocturnal illumination. Common opossums may not be under such great predation risk. Additionally, armadillos exhibited a smaller, but surprising, activity peak at the middle of the night during the full moon. Armadillos have poor vision (Medri, Mourão & Rodrigues, 2006) and were reported to be less active in enlightened nights in order to be less exposed to predators they cannot see (Harmsen *et al*., 2010). Still, they may be able to get foraging benefits from being active at such risky time of the night during full moon. Gursky (2003) reported greater insect availability in moonlit nights. Considering this, being active at such time may be associated with high apprehension periods (Brown, 1999) but represent a major increase in foraging efficiency for armadillos.

Prey behaviour is likely to be also affected by the moon during the first and last quarters due to the different times of moon transit in these two moon phases. Although the temporal distribution of records is not different between these two phases, prey seemed to respond to variations of predation risk allocating their major activity peaks to times before and after the moon transit. Prey concentrate their activities in lower predation risk periods when the high risk periods are frequent (Lima & Bednekoff, 1999). The greater diurnal activity of red brocket deer during the last quarter is therefore likely to minimise the risk of being predated upon by pumas, since the activity of these cats was mostly nocturnal. In addition, the even record distribution of pumas across the moon cycle may also pose a major threat for prey due to the encounters unpredictability, forcing prey to allocate the

activity to the darker periods of the night, when they feel safer. Thus, we suggest that prey can shift the temporal distribution of their behaviour under different moon phases in response to higher predation risk, allocating their activity to periods when it is lower. The avoidance of the night hours with maximum illumination is likely to hinder the hunting efficiency of pumas and allows prey to be more relaxed and carry out their activities more readily in darker times.

This study provides the first insights concerning the effect of the moon phases on the schedules of medium and large-sized mammals. Further research on habitat use of medium and large-sized mammals will provide more reliable data and knowledge concerning the coexistence of these taxa with their predators.

CONCLUSION

Prey may use moonlight as a surrogate of predation risk. In the Amazon *terra-firme* forests the variations of predation risk during the moon cycle seem to affect both the amount of records and time schedules of cats' prey in different moon phases. One could hypothesize that the moonlight effect on mammal activity patterns in rainforest would not be as high as in opened areas due to the canopy cover. That does not seem to be the case, however, since moonlight appears to affect both habitat use and activity patterns, not only in our study sites, but in other rainforest locations as well. This is probably due to some canopy gaps. Generally, in darker nights prey appear to be more relaxed, since they remain less visible to predators. Differently, the activity during enlightened nights poses greater threat to prey because they can be spotted by predators more easily. It is therefore likely that visual abilities also play a major role in activity patterns. Our findings suggest that, in bright nights, prey with poor eyesight can suppress their activity or shift its temporal distribution, through activity allocation, to darker periods of the night in response to increased predation risk. On the other hand prey with better visual sensory systems may get a positive trade-off between the risks and benefits of being active at more enlightened times but, in turn, be more exposed to predator attacks and, thus, favour their hunting success.

It seems that the temporal distribution of prey activity is based in a trade-off between safety and foraging benefits. As for cats, although they spend large amounts of time searching for prey, their hunting efficiency is boosted in bright nights. Our findings provide the first insights concerning the effect of the moon cycle on the temporal activity and dynamics of predators and prey in *terra-firme* forests of Central Amazon. Further research on other niche axis of the mammalian community on this region is therefore needed concerning the coexistence between prey and predators.

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